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# Disparate rates, differing fates: Tempo and mode of evolution changed from the Precambrian to the Phanerozoic

(cyanobacteria/hypobradytely/living fossils)

J. WILLIAM SCHOPF

Center for the Study of Evolution and the Origin of Life, Department of Earth and Space Sciences, Molecular Biology Institute, and Institute of Geophysics and Planetary Physics, University of California, Los Angeles, CA 90024

**ABSTRACT** Over the past quarter century, detailed genus- and species-level similarities in cellular morphology between described taxa of Precambrian microfossils and extant cyanobacteria have been noted and regarded as biologically and taxonomically significant by numerous workers worldwide. Such similarities are particularly well documented for members of the Oscillatoriaceae and Chroococcaceae, the two most abundant and widespread Precambrian cyanobacterial families. For species of two additional families, the Entophysalidaceae and Pleurocapsaceae, species-level morphologic similarities are supported by in-depth fossil-modern comparisons of environment, taphonomy, development, and behavior. Morphologically and probably physiologically as well, such cyanobacterial “living fossils” have exhibited an extraordinarily slow (hypobradytelic) rate of evolutionary change, evidently a result of the broad ecologic tolerance characteristic of many members of the group and a striking example of G. G. Simpson’s [Simpson, G. G. (1944) *Tempo and Mode in Evolution* (Columbia Univ. Press, New York)] “rule of the survival of the relatively unspecialized.” In both tempo and mode of evolution, much of the Precambrian history of life—that dominated by microscopic cyanobacteria and related prokaryotes—appears to have differed markedly from the more recent Phanerozoic evolution of megascopic, horotelic, adaptationally specialized eukaryotes.

When G. G. Simpson wrote *Tempo and Mode* (1), fossil evidence of the history of life consisted solely of that known from sediments of the Phanerozoic eon, the most recent 550 million years (Ma) of geologic time (Fig. 1). Thus, Simpson’s views of the evolutionary process were based necessarily on Phanerozoic life—the familiar progression from seaweeds to flowering plants, from trilobites to humans—a history of relatively rapidly evolving, sexually reproducing plants and animals successful because of their specialized organ systems (flowers, leaves, teeth, limbs) used to partition and exploit particular environments. In short, Simpson elucidated “normal evolution” played by the “normal rules” of the game—speciation, specialization, extinction.

Although certainly applicable to the megascopic eukaryotes of the Phanerozoic, there is reason to question whether these well-entrenched rules apply with equal force to the earlier and very much longer Precambrian phase of microbe-dominated evolutionary history (Fig. 1). In place of sexual multicellular plants and animals, the biota throughout much of the Precambrian was dominated by simple nonsexual prokaryotes. Rather than evolving rapidly, many Precam-

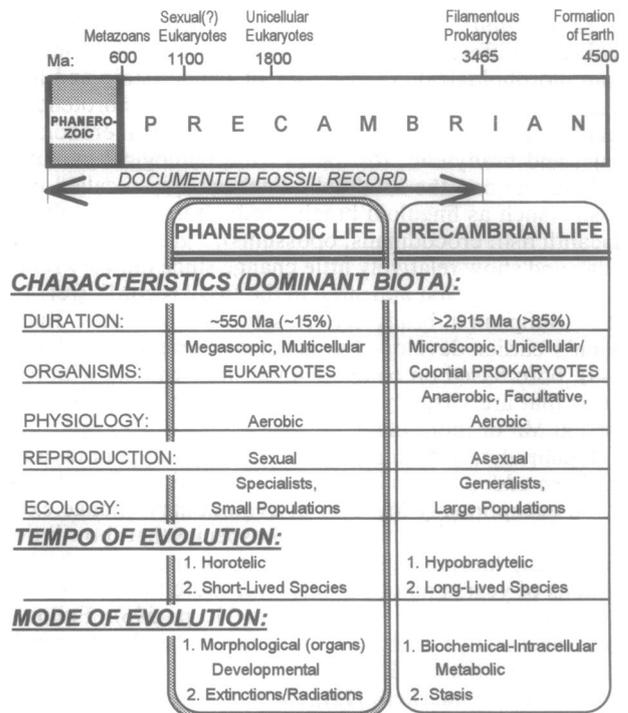


FIG. 1. Comparison of the Phanerozoic and Precambrian histories of life.

brian microbes evidently evolved at an astonishingly slow pace. And instead of having specialized organ systems for exploitation of specific ecologic niches, members of the most successful group of these early-evolving microorganisms—photoautotrophic cyanobacteria—were ecologic generalists, able to withstand the rigors of a wide range of environments. In contrast with normal evolution, the “primitive rules” of prokaryotic evolution appear to have been speciation, generalization, and exceptionally long-term survival.

That there is a distinction in evolutionary tempo and mode between the Phanerozoic and Precambrian histories of life is not a new idea (2), but it is one that has recently received additional impetus (3) and therefore deserves careful scrutiny. However, evaluation of this generalization hinges critically on the quality and quantity of the fossil evidence available, and because active studies of the Precambrian fossil record have been carried out for little more than a quarter century (4) a thorough comparison of the early history of life with that of later geologic time is not yet

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Abbreviations: Ma, million year(s); Ga, billion year(s).

possible. Therefore, as a first approximation, the approach used here is to analyze the known fossil record of Precambrian cyanobacteria: well-studied, widespread, abundant, commonly distinctive, and evidently dominant members of the early prokaryotic biota. Microscopic fossils regarded as members of other prokaryotic groups are also known from the Precambrian (5, 6), but their documented record is minuscule. Hence, conclusions drawn here about the early fossil record apply strictly to free-living cyanobacteria, the evolutionary history of which may or may not be representative of prokaryotes in general. To evaluate the generalization, two central questions must be addressed. First, was the tempo of Precambrian cyanobacterial evolution markedly slower than that typical of Phanerozoic eukaryotes? Second, if so, how can this difference be explained?

### Tempos of Evolution

In *Tempo and Mode*, Simpson (1) coined terms for three decidedly different rate distributions in evolution, inferred from morphological comparisons of Phanerozoic and living taxa: tachytelic, for "fast"-evolving lineages; horotelic, the standard rate distribution, typical of most Phanerozoic animals; and bradytelic, for "slow" morphological evolution. Included among the bradytelic lineages are so-called living fossils (such as linguloid brachiopods, horseshoe crabs, coelacanth fish, crocodilians, opossums), "groups that survive today and show relatively little change since the very remote time when they first appeared in the fossil record" (ref. 1, p. 125). Simpson's bradytely closely approximates Ruedemann's earlier developed concept of "arrested evolution" (7-9), both based on comparison of modern taxa with fossil forms that are virtually indistinguishable in morphology but are 100 Ma or more older.

**Hypobradytely.** Recently, a fourth term—hypobradytely—has been added to this list of rate distributions (10) "to refer to the exceptionally low rate of evolutionary change exhibited by cyanobacterial taxa, morphospecies that show little or no evident morphological change over many hundreds of millions of years and commonly over more than one or even two thousand million years" (ref. 11, p. 596). Following Simpson's lead, hypobradytely is based strictly on morphological comparison of living and fossil taxa. Other data, such as chemical biomarkers (11), carbon isotopic compositions (12), and environmental distributions (13), can provide insight on the paleophysiology of fossil cyanobacteria, but the concept of hypobradytely does not necessarily imply genomic, biochemical, or physiological identity between modern and fossil taxa. The concept can be applied to cyanobacteria because the morphologic descriptors and patterns of cell division used to differentiate taxa at various levels of the taxonomic hierarchy are preservable in ancient sediments (6, 11, 13, 14); as emphasized by Knoll and Golubic (ref. 13, p. 453), "Essentially all of the salient morphological features used in the taxonomic classification of living cyanobacteria can be observed in well-preserved microfossils."

Interpreted as evidencing exceptional "morphological evolutionary conservatism," detailed genus- and species-level similarities between Precambrian and extant cyanobacteria, both for filamentous (oscillatoriacean) and spheroidal (chroococcacean) taxa, were documented as early as 1968 (15). Since that time, such similarities have been recognized repeatedly. Indeed, it has become common practice for Precambrian paleobiologists to coin generic names intended to denote similarity or inferred identity between ancient cyanobacterium-like fossils and their modern morphological analogs by adding appropriate prefixes (palaeo-, eo-) or suffixes (-opsis, -ites) to the names of living cyanobacterial genera (Table 1). The validity of such comparisons is variable, and although more than 40 such fossil namesakes have

been proposed (for genera referred to diverse cyanobacterial families; Table 1), their use does not in and of itself constitute compelling evidence of hypobradytely.

**Caveats.** Application of the concept of hypobradytely is not without potential pitfalls, three of which deserve particular mention. First, because of the enormous span of Precambrian time (Fig. 1), and despite the notable paleontological progress of recent years (4), early biotic history is as yet very incompletely documented. In comparison with the vastly better documented record of Phanerozoic organisms—and even in geologic units of the Proterozoic (2500–550 Ma in age), by far the most studied portion of the Precambrian—the known cyanobacterial fossil record is scanty (for filamentous species amounting to  $\approx 21$  taxonomic occurrences per 50-Ma-long interval and, for spheroidal species,  $\approx 46$  occurrences; refs. 5 and 16). Second, assignment of some Precambrian microbial fossils (evidently  $<10\%$ ) to the cyanobacteria can be quite uncertain, a problem that applies especially to minute morphologically simple forms (atypically small-diameter oscillatoriaceans and chroococcaceans, for example), which in the fossil state are essentially indistinguishable from various noncyanobacterial prokaryotes (6). Third, lack of change in the external form of morphologically simple prokaryotes may not necessarily reflect evolutionary stasis of their internal physiological machinery (the so-called Volkswagen syndrome; ref. 17). This last problem is especially difficult to evaluate, but it may not be of overriding importance—from early in the Proterozoic to the present, the same cyanobacterial families and many of the same (morphologically defined) genera and even species appear to have inhabited the same or closely similar environments, patterns of distribution that "provide proxy information on physiological attributes" (ref. 13, p. 451).

### Cyanobacterial Hypobradytely

Are cyanobacteria hypobradytelic? Data bearing on this question fall into two classes. First, a large amount of evidence indicates that the proposition is plausible, in fact likely to be correct, but, because of a lack of accompanying relevant (chiefly environmental) information, this evidence is not fully compelling. Second, a small number of in-depth studies firmly support the proposition, but because of their limited number and restricted taxonomic scope these studies do not establish the proposition generally. Considered together, however, the two classes of data present a strong case.

**Evidence of Plausibility.** Shown in Fig. 2 are paired examples of morphologically comparable Proterozoic and living cyanobacteria including specimens illustrating the rather commonly cited (15, 18–20) similarity between fossil *Palaeolyngbya* (Fig. 2B) and *Lyngbya* (Fig. 2A), its modern morphological counterpart. Numerous other genus- and species-level comparisons have been drawn [for example, between  $\approx 850$ -Ma-old *Cephalophytarion grande* and the modern oscillatoriacean *Microcoleus vaginatus* (15, 20); and between  $\approx 2$ -billion year (Ga)-old *Eosynechococcus moorei* and the living chroococcacean *Gloeotheca coerulea* (*Gloeobacter violaceus*) (19)]. Examples such as these—and the fact that over the past quarter century such similarities have been noted repeatedly and regarded as biologically and taxonomically significant by a large number of workers in many countries (Table 1)—provide a powerful argument for the plausibility of cyanobacterial hypobradytely.

Plausibility of the concept is similarly indicated by quantitative studies recently carried out on large assemblages of modern and Precambrian microbes. Morphometric data (for such attributes as cell size, shape, and range of variability; colony form; sheath thickness and structure) were compiled for 615 species and varieties of living cyanobacteria (6) as well as for an extensive worldwide sample of Proterozoic

Table 1. Precambrian generic namesakes, coined by various authors to suggest similarity to modern cyanobacterial genera (16)

| Modern genus             | Precambrian genus; author(s)                             | No. of species | Year published | Country of author(s) |
|--------------------------|--|----------------|----------------|----------------------|
| Family Oscillatoriaceae  |  |                |                |                      |
| <i>Lyngbya</i>           | <i>Palaeolyngbya</i> ; Schopf                            | 11             | 1968           | USA                  |
| <i>Lyngbya</i>           | cf. <i>Lyngbya</i> ; Schopf, Xu, Xu, and Hsu             | 1              | 1984           | USA, China           |
| <i>Microcoleus</i>       | <i>Eomicrocoleus</i> ; Horodyski and Donaldson           | 1              | 1980           | USA, Canada          |
| <i>Oscillatoria</i>      | <i>Archaeosclatoria</i> ; Schopf                         | 3              | 1993           | USA                  |
| <i>Oscillatoria</i>      | <i>Oscillatoriopsis</i> ; Schopf                         | 22             | 1968           | USA                  |
| <i>Oscillatoria</i>      | <i>Oscillatorites</i> ; Schepeleva                       | 1              | 1960           | Russia               |
| <i>Oscillatoria</i>      | cf. <i>Oscillatoria</i> ; Schopf and Sovietov            | 1              | 1976           | USA, Russia          |
| <i>Phormidium</i>        | <i>Eophormidium</i> ; Xu                                 | 3              | 1984           | China                |
| <i>Schizothrix</i>       | <i>Schizothrix</i> ; Edhom                               | 1              | 1973           | Canada               |
| <i>Schizothrix</i>       | <i>Schizothropsis</i> ; Xu                               | 1              | 1984           | China                |
| <i>Spirulina</i>         | <i>Palaeospirulina</i> ; Edhorn                          | 2              | 1973           | Canada               |
| <i>Spirulina</i>         | <i>Spirillinema</i> ; Shimron and Horowitz               | 1              | 1972           | Israel               |
| <i>Spirulina</i>         | aff. <i>Spirulina</i> ; Schopf and Blacic                | 1              | 1971           | USA                  |
| Family Chroococcaceae    |  |                |                |                      |
| <i>Anacystis</i>         | <i>Palaeoanacystis</i> ; Schopf                          | 8              | 1968           | USA                  |
| <i>Aphanocapsa</i>       | <i>Aphanocapsaopsis</i> ; Maithy and Shukla              | 2              | 1977           | India                |
| <i>Aphanocapsa</i>       | <i>Eoaphanocapsa</i> ; Nyberg and Schopf                 | 1              | 1984           | USA                  |
| <i>Aphanothece</i>       | <i>Eoaphanothece</i> ; Xu                                | 1              | 1984           | China                |
| <i>Chroococcus</i>       | <i>Chroococcus</i> -like; Mendelson and Schopf           | 1              | 1982           | USA                  |
| <i>Eucapsis</i>          | <i>Eucapsamorpha</i> ; Golovenoc and Belova              | 1              | 1985           | Russia               |
| <i>Eucapsis</i>          | <i>Eucapsis</i> ?; Licari, Cloud, and Smith              | 1              | 1969           | USA                  |
| <i>Gloeocapsa</i>        | <i>Eogloeocapsa</i> ; Golovenoc and Belova               | 1              | 1984           | Russia               |
| <i>Gloeocapsa</i>        | <i>Gloeocapsa</i> -like; Zhang                           | 1              | 1985           | China                |
| <i>Merismopedia</i>      | cf. <i>Merismopedia</i> ; Schopf and Fairchild           | 1              | 1973           | USA, Brazil          |
| <i>Microcystis</i>       | <i>Eomicrocystis</i> ; Maithy                            | 2              | 1975           | India                |
| <i>Microcystis</i>       | <i>Microcystopsis</i> ; Xu                               | 1              | 1984           | China                |
| <i>Microcystis</i>       | <i>Palaeomicrocystis</i> ; Maithy                        | 2              | 1975           | India                |
| <i>Synechococcus</i>     | <i>Eosynechococcus</i> ; Hofmann                         | 13             | 1976           | Canada               |
| Family Entophysalidaceae |  |                |                |                      |
| <i>Entophysalis</i>      | <i>Eoentophysalis</i> ; Hofmann                          | 6              | 1976           | Canada               |
| Family Pleurocapsaceae   |  |                |                |                      |
| <i>Hyella</i>            | <i>Eohyella</i> ; Zhang and Golubic                      | 4              | 1987           | China, USA           |
| <i>Myxosarcina</i>       | cf. <i>Myxosarcina</i> ; Schopf and Fairchild            | 1              | 1973           | USA, Brazil          |
| <i>Pleurocapsa</i>       | <i>Eopleurocapsa</i> ; Liu                               | 1              | 1982           | China                |
| <i>Pleurocapsa</i>       | <i>Palaeopleurocapsa</i> ; Knoll, Barghoorn, and Golubic | 6              | 1975           | USA                  |
| Family Nostocaceae       |  |                |                |                      |
| <i>Anabaena</i>          | <i>Anabaenidium</i> ; Schopf                             | 4              | 1968           | USA                  |
| <i>Aphanizomenon</i>     | <i>Palaeoaphanizomenon</i> ; Mikhailova                  | 1              | 1986           | Russia               |
| <i>Isocystis</i>         | <i>Palaeoisocystis</i> ; Xu                              | 2              | 1984           | China                |
| <i>Nostoc</i>            | <i>Nostocomorpha</i> ; Sin and Liu                       | 1              | 1978           | China                |
| <i>Nostoc</i>            | <i>Palaeonostoc</i> ; Nautiyal                           | 1              | 1980           | India                |
| <i>Nostoc</i>            | <i>Veteronostocale</i> ; Schopf                          | 2              | 1968           | USA                  |
| Family Rivulariaceae     |  |                |                |                      |
| <i>Calothrix</i>         | <i>Palaeocalothrix</i> ; Xu                              | 2              | 1984           | India                |
| <i>Rivularia</i>         | <i>Primorivularia</i> ; Edhorn                           | 3              | 1973           | Canada               |
| Family Scytonemataceae   |  |                |                |                      |
| <i>Plectonema</i>        | <i>Eoplectonema</i> ; Liu                                | 1              | 1984           | China                |
| <i>Scytonema</i>         | <i>Palaeoscytonema</i> ; Edhorn                          | 5              | 1973           | Canada               |

cyanobacterium-like microfossils (16), both filamentous (650 taxonomic occurrences in 160 geologic formations) and spheroidal (1400 occurrences in 259 formations). To avoid confusion stemming from variations in taxonomic practice, fossils having the same or similar morphology (regardless of their binomial designations) were grouped together as informal species-level morphotypes designed to have ranges of morphologic variability comparable to those exhibited by living cyanobacterial species (5). Of the 143 informal species of filamentous microfossils thus recognized, 37% are essentially indistinguishable in morphology from established species of living (oscillatoriacean) cyanobacteria (5). Similarly, 25% of the 120 informal taxa of spheroidal fossil species have modern species-level (largely chroococcacean) morphological counterparts (5). Virtually all of the fossil morphotypes are referable to living genera of cyanobacteria, and the

patterns and ranges of size distribution exhibited by taxa of cylindrical sheath-like Proterozoic fossils are essentially identical to those of the tubular sheaths that encompass trichomes of modern oscillatoriacean species (Fig. 3).

About half of the  $\approx 2000$  fossil occurrences included in this morphometric study were reported from cherty carbonate stromatolites, with the remainder from clastic shales and siltstones. Data regarding the specific environmental settings represented by these lithologies are available for very few of the  $>300$  fossiliferous geologic units considered. With varying degrees of uncertainty (but almost always without firm evidence), most of these strata have been assumed to represent relatively shallow water coastal marine facies, ranging from sabkhas and lagoons to mud flats and intertidal carbonate platforms. In such environments today, mat-building oscillatoriaceans (predominantly *Oscillatoria*, *Lyngbya*, *Phormidium*, *Spirulina*, *Microco-*

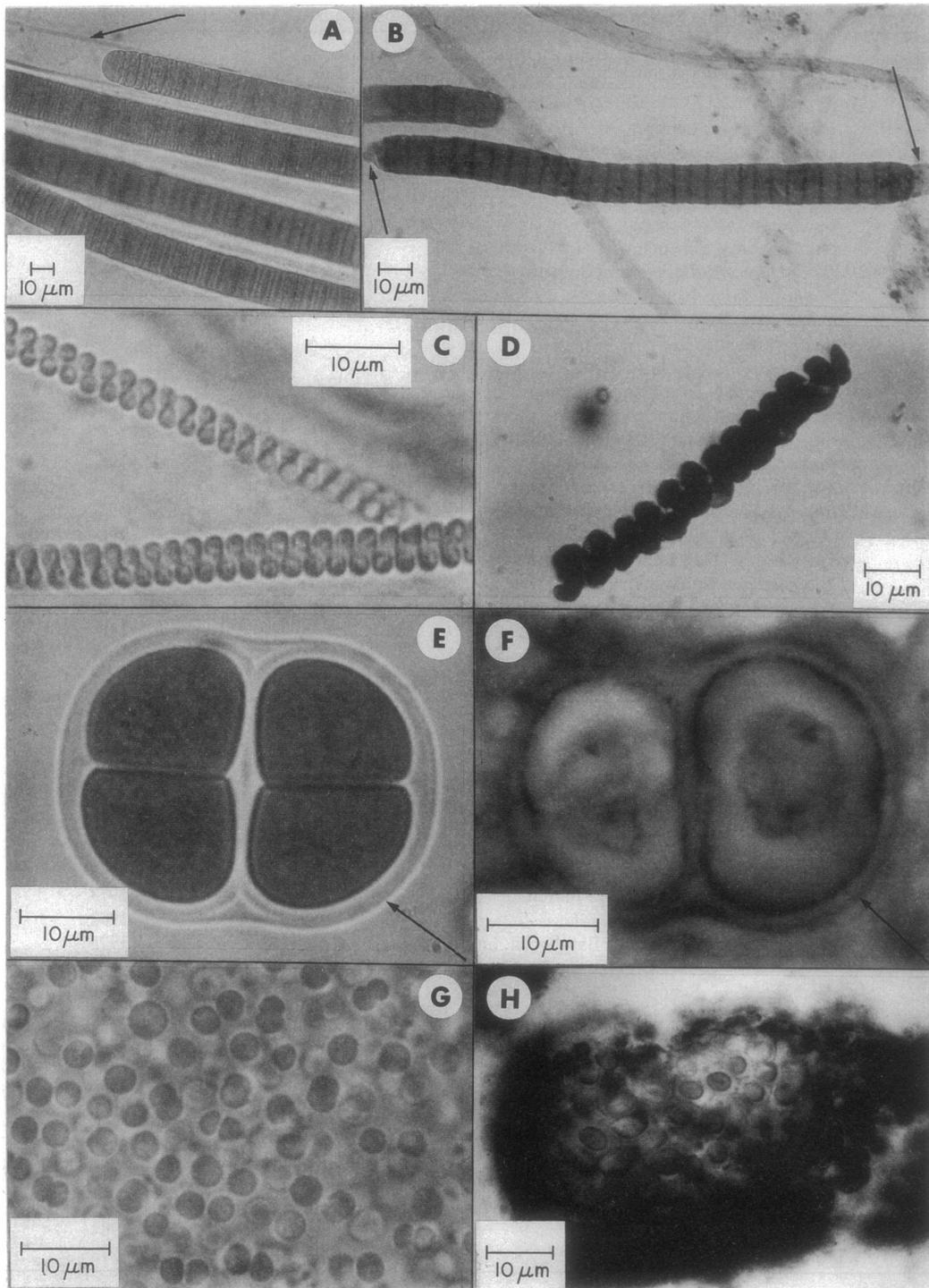


FIG. 2. Comparison of living and Precambrian cyanobacteria. Living examples (A, C, E, and G) are from mat-building stromatolitic communities of northern Mexico. (A) *Lyngbya* (Oscillatoriaceae), encompassed by a cylindrical mucilaginous sheath (arrow). (B) *Palaeolyngbya*, similarly ensheathed (arrows), from the  $\approx 950$ -Ma-old Lakhanda Formation of eastern Siberia. (C) *Spirulina* (Oscillatoriaceae). (D) *Heliconema*, a *Spirulina*-like cyanobacterium from the  $\approx 850$ -Ma-old Miroedikha Formation of eastern Siberia. (E) *Gloeocapsa* (Chroococcaceae), a four-celled colony having a thick distinct encompassing sheath (arrow). (F) *Gloeodiniopsis*, a similarly sheath-enclosed (arrow) *Gloeocapsa*-like cyanobacterium, from the  $\approx 1550$ -Ma-old Satka Formation of southern Bashkiria. (G) *Entophysalis* (Entophysalidaceae). (H) *Eoentophysalis*, an *Entophysalis*-like colonial cyanobacterium from the  $\approx 2$ -Ga-old Belcher Group of Northwest Territories, Canada (21).

*leus*, and *Schizothrix*) and subsidiary chroococcaceans (such as *Chroococcus*, *Aphanocapsa*, *Aphanothece*, and *Synechococcus*) are common (14, 22, 23). As is shown in Fig. 4, these same two families, as well as morphotypes referable to most of the same genera, are similarly common among the fossil taxa having living species-level counterparts.

In view of these data, it is difficult not to conclude that "the biological constitution of [Proterozoic] microbial mat com-

munities was probably quite similar to that of modern communities in comparable environments" (ref. 24, p. 411).

**In-Depth Studies.** In addition to studies of cellular morphology and likely (but not firmly established) broad-scope environmental comparisons, what is needed to move the hypobradytelic hypothesis from the plausible to the compelling are supporting data on the paleoenvironment and taphonomy of the fossils in question (13). A number of such

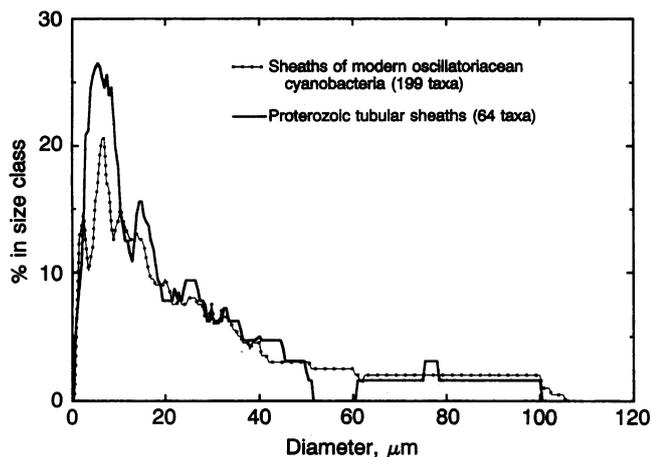


FIG. 3. Comparison of patterns and ranges of size distribution of cylindrical sheath-like Precambrian fossils with those of the tubular sheaths of living oscillatoriacean cyanobacteria (6).

in-depth studies have been carried out (21, 25–28), focusing on fossil representatives of two cyanobacterial families, the Entophysalidaceae and the Pleurocapsaceae, members of which are decidedly more distinctive morphologically than are the oscillatoriaceans and chroococcaceans discussed above. Golubic and Hofmann (21) compared  $\approx 2$ -Ga-old *Eoentophysalis belcherensis* (Fig. 2H) with two modern entophysalidaceans (*Entophysalis major* and *Entophysalis granulosa*). They showed that not only are the fossil and modern species morphologically comparable (in cell shape and in form and arrangement of originally mucilaginous cellular envelopes) and that they exhibit similar frequency distributions of dividing cells and essentially identical patterns of cellular development (resulting from cell division in three perpendicular planes), but also that both taxa form microtexturally similar stromatolitic structures in comparable intertidal to shallow marine environmental settings, that they undergo similar postmortem degradation sequences, and that they occur in microbial communities that are comparable in both species composition and biological diversity. In a subsequent detailed study, Knöll and Golubic (26) compared the morphology, cell division patterns, ecology, and postmortem degradation sequences of a second Precambrian entophysalidacean ( $\approx 850$ -Ma-old *Eoentophysalis cumulus*) with those of modern *E. granulosa* and concluded that the fossil “microorganism is identical in all its salient char-

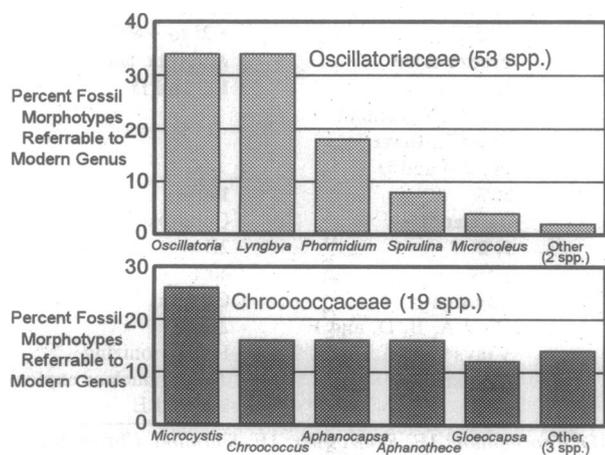


FIG. 4. Distribution among modern oscillatoriacean and chroococcacean genera of Precambrian species-level morphotypes having living morphological counterparts (5, 6).

acteristics to members of the extant [cyanobacterial] genus” (ref. 26, p. 125).

Several species of fossil and living pleurocapsaceans have also been compared in detail. *Polybessurus bipartitus*, first reported from  $\approx 770$ -Ma-old stromatolites of South Australia (29, 30), is a morphologically distinctive, gregarious, cylindrical fossil pleurocapsacean composed of stacked cup-shaped envelopes often extended into long tubes oriented predominantly perpendicular to the substrate. Specimens of this taxon occurring in rocks of about the same age in East Greenland were interpreted by Green *et al.* (27) to be “a close morphological, reproductive, and behavioral counterpart” to populations of a species of the pleurocapsacean *Cyanostylon* present “in Bahamian environments similar to those in which the Proterozoic fossils occur” (ref. 27, p. 928). A second fossil pleurocapsacean described from the  $\approx 770$ -Ma-old Australian deposit (*Palaeopleurocapsa wopfnerii*) has been compared by Knöll *et al.* (25) with its living morphological and ecological analog (*Pleurocapsa fuliginosa*) and regarded as “further evidence of the evolutionary conservatism of [cyanobacteria]” (ref. 25, p. 2492). Two other species of morphologically distinctive fossil pleurocapsaceans (the endolithic taxa *Eohyella dichotoma* and *Eohyella rectroclada*), cited as “compelling examples of the close resemblance between Proterozoic prokaryotes and their modern counterparts” (ref. 31, p. 857), have been described by Green *et al.* (28) from the East Greenland geologic sequence as being “morphologically, developmentally, and behaviorally indistinguishable” from living *Hyella* species of the Bahama Banks (ref. 28, pp. 837–838).

These in-depth studies of entophysalidaceans and pleurocapsaceans—involving analyses of environment, taphonomy, development, and behavior, in addition to cellular morphology—provide particularly convincing evidence of species-specific fossil-modern similarities.

**Cyanobacteria Are Hypobradytelic.** Thus, numerous workers worldwide have noted and regarded as significant the detailed similarities in cellular morphology between Precambrian and extant cyanobacteria (Table 1; Fig. 2). A substantial fraction of known Proterozoic oscillatoriacean and chroococcacean cyanobacteria have living species-level morphological counterparts (Fig. 4), and almost all such fossils are referable to living cyanobacterial genera. And in-depth studies of several fossil-modern species pairs of morphologically distinctive entophysalidaceans and pleurocapsaceans permit detailed comparison of morphology, development, population structure, environment, and taphonomy, all of which show that for at least these taxa, ancient and modern cyanobacteria are essentially indistinguishable in salient characteristics.

Taken together, these observations support an obvious conclusion—the morphology (and evidently the physiology as well) of diverse taxa belonging to major cyanobacterial families evolved little or not at all over hundreds of millions, indeed thousands of millions of years. In comparison with the later history of life, this widespread hypobradytely is surprising. In Phanerozoic evolution, bradytelic stasis is notable principally because of its rarity (1, 7–9), but in the Precambrian it seems to have been a general phenomenon characteristic of a group of prokaryotic microorganisms that dominated the Earth’s biota, possibly even as early as 3.5 Ga ago (32). Why have cyanobacteria evidently changed so little over their exceedingly long evolutionary history?

#### Survival of the Ecologically Unspecialized

To understand the underlying causes of cyanobacterial hypobradytely, it is instructive to review Simpson’s thoughtful analysis in *Tempo and Mode*, for although he was unaware of the Precambrian prokaryotic fossil record, Simpson was

much interested in slowly evolving (bradytelic) Phanerozoic lineages. In addition to noting (but dismissing) the possibility that "asexual reproduction (as inhibiting genetic variability)" might be conducive to slow evolution (ref. 1, p. 137), he singled out two principal factors: large population size (p. 138), and ecologic versatility, an exceptional degree of adaptation "to some ecological position or zone with broad . . . selective limits . . . a particular, continuously available environment" (pp. 140–141). Because unusually slow evolution involves "not only exceptionally low rates of [evolutionary change] but also survival for extraordinarily long periods of time" (p. 138), and because "more specialized phyla tend to become extinct before less specialized" (p. 143), Simpson proposed "the rule of the survival of the relatively unspecialized" (p. 143).

Although intended by Simpson to apply to Phanerozoic organisms, chiefly animals, these same considerations (with the addition of asexual reproduction) apply to Precambrian cyanobacteria. First, with regard to reproduction, cyanobacteria are strictly asexual, lacking even the parasexual processes known to occur in some other prokaryotes. Given the remarkable longevity of the cyanobacterial lineage and moderate or even low rates of mutation, however, the absence of sexually generated genetic variability cannot be the sole explanation for their hypobradytely. Second, like virtually all free-living microorganisms, cyanobacteria typically occur in local populations of large size. Coupled with their ease of dispersal (via water currents, wind, and hurricanes, for example) and for many species a resulting very wide (essentially cosmopolitan) geographic distribution, their large populations can also be presumed to have played a role in their evolutionary stasis (Fig. 1). Third, and probably most important, however, is the ecologic versatility of the group.

Summarized in Table 2 are known ranges of survivability (and of growth under natural conditions) for modern oscil-

latoriaceans and chroococcaceans, the most primitive (62) and commonly occurring (6) Precambrian cyanobacterial families. Similar tolerance is also exhibited by members of other cyanobacterial families. For example, a nostocacean was revived after more than a century of storage in a dried state (44) and a scytonematacean is reported to have maintained growth at pH 13 (37). Thus, cyanobacteria exhibit notable ecologic flexibility, and even though no single oscillatoriacean or chroococcacean species is known to be capable of tolerating the total range of observed growth conditions (for example, thermophiles dominant in 70°C waters rarely grow below 50°C, and species adapted to highly alkaline lakes do not occur in acid hot springs), both groups include impressive ecologic generalists, able to thrive in virtually all present-day widespread environments (Table 2). Moreover, many of the oscillatoriacean and chroococcacean genera for which wide ecologic tolerance has been demonstrated (Table 2) are the same as those having species-level Precambrian-extant counterparts (Fig. 4). Finally, numerous cyanobacteria, including both oscillatoriaceans and chroococcaceans (63), are capable of fixing atmospheric nitrogen; provided with light, CO<sub>2</sub>, a source of electrons (H<sub>2</sub>, H<sub>2</sub>S, H<sub>2</sub>O), and a few trace elements, such cyanobacteria are highly effective colonizers, able to invade and flourish in a wide range of habitats.

The wide ecologic tolerance of cyanobacteria is almost certainly a product of their early evolutionary history. Fossil evidence suggests that oscillatoriaceans (32) and chroococcaceans (64, 65) were extant as early as ≈3.5 Ga ago. If so, they must have originated and initially diversified in an oxygen-deficient environment, one lacking an effective UV-absorbing ozone layer. In such an environment, the ability to photosynthesize at low light intensities (Table 2) coupled with the presence of gas vesicles to control buoyancy (66) would have permitted planktonic cyanobacteria to avoid deleterious

Table 2. Survival [and growth under natural conditions (boldface)] of oscillatoriacean and chroococcacean cyanobacteria (33–61)

|                  | 1–5 $\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ | <b>50–60 <math>\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}</math></b> | <b>&gt;2000 <math>\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}</math></b> |                         |
|------------------|---|---|--|-------------------------|
| Light intensity  | 1–5 $\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ | <b>50–60 <math>\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}</math></b> | <b>&gt;2000 <math>\mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^{-2}</math></b> |                         |
| Conditions       | Cultures  | <b>Optimum growth</b>   | <b>Intertidal zone</b>   |                         |
| Genera           | 1C; 2 E and F   | 1, 2  | 1, 2   |                         |
| Total salinity   | <0.001–0.1%   | 3.5%  | 27.5%  | 100–200%                |
| Conditions       | <b>Freshwater</b>                                     | <b>Marine</b>   | <b>Great Salt Lake</b>   | Salterns                |
| Genera           | 1, 2  | 1, 2  | 2D   | 1 B–D and F; 2F         |
| Acidity/basicity | pH 4  | pH 7–10   | pH 10–11   |                         |
| Conditions       | <b>Hot springs</b>                                    | <b>Optimum growth</b>   | <b>Alkaline lakes</b>  |                         |
| Genera           | 2F  | 1, 2  | 1F; 2E   |                         |
| High temperature | 55–70°C   | 74°C  | 111°C  | 112°C                   |
| Conditions       | <b>Hot springs</b>                                    | <b>Hot springs</b>  | Dried  | Dried                   |
| Genera           | 1 C, D, and F; 2 C and F                              | 2F  | 1E   | 1B                      |
| Low temperature  | –269°C  | –196°C  | –55°C  | –2° to +4°C             |
| Conditions       | Liquid He   | Liquid H <sub>2</sub>   | Freeze-dried   | <b>Antarctic lakes</b>  |
| Genera           | 1C  | 1 D and E   | 1A   | 1 C and D               |
| Desiccation      | 88  | 82 yr   | <b>Absence of rainfall</b>   |                         |
| Conditions       | Dried   | Dried   | <b>Atacama Desert</b>  |                         |
| Genera           | 1C  | 2E  | 1E; 2 B and D  |                         |
| Oxygen           | <0.01%  | 1%  | 20%  | 100%                    |
| Conditions       | <b>Anoxic lakes</b>                                   | <b>Blooms, muds</b>   | <b>Ambient O<sub>2</sub></b>   | Cultures                |
| Genera           | 1, 2  | 1, 2  | 1, 2   | 2B                      |
| Carbon dioxide   | 0.001%  | 0.035%  | 3.5%   | 40%                     |
| Conditions       | Cultures  | <b>Ambient CO<sub>2</sub></b>   | Cultures   | Cultures                |
| Genera           | 2B  | 1, 2  | 1E; 2 A, B, D, and F   | 2B                      |
| Radiation        | <b>Ultraviolet</b>                                    | X-rays  | $\gamma$ -rays   | Highly ionizing         |
| Conditions       | <b>290–400 nm*</b>                                    | 200 kr <sup>†</sup>   | 2560 kr <sup>‡</sup>   | Thermonuclear explosion |
| Genera           | 1 A and E; 2C   | 1C  | 1B   | 1 B and E               |

Oscillatoriacean genera: 1A, *Lyngbya*; 1B, *Microcoleus*; 1C, *Oscillatoria*; 1D, *Phormidium*; 1E, *Schizothrix*; 1F, *Spirulina*. Chroococcacean genera: 2A, *Agmenellum*; 2B, *Anacystis*; 2C, *Aphanocapsa*; 2D, *Coccochloris*; 2E, *Microcystis*; 2F, *Synechococcus*.

\*Absorbed by scytonemin pigment in encompassing sheaths.

<sup>†</sup>Twice as resistant as eukaryotic microalgae.

<sup>‡</sup>Ten times as resistant as eukaryotic microalgae.

UV by inhabiting the deep oceanic photic zone, just as *Synechococcus* does today. Similarly, numerous characteristics of living benthic mat-building cyanobacteria—effective DNA repair mechanisms, synthesis of UV-absorbing scytonemin, secretion of copious extracellular mucilage, phototactic motility, adherence to substrates, stromatolitic mat formation—initially may have been adaptations to cope with a high UV flux in near-shore shallow water settings. Adaptive radiation in an early oxygen-deficient environment is also suggested by the ability of cyanobacteria to live in either the presence or absence of oxygen (Table 2), their capability to switch between oxygenic and anoxygenic photosynthesis (67), the occurrence of oxygen-sensitive nitrogenase in many taxa (63), and the restriction of nitrogenase-protecting heterocysts to late-evolving members of the group (62). In addition, both the low affinity of cyanobacterial ribulose-bisphosphate carboxylase for CO<sub>2</sub> and the presence of intracellular CO<sub>2</sub>-concentrating mechanisms (68) may reflect initial adaptation of the lineage to a CO<sub>2</sub>-rich primordial environment (69).

Finally, the remarkable hardiness of cyanobacteria—their ability to survive wide ranges of light intensity, salinity, temperature, and pH as well as prolonged desiccation and intense radiation (Table 2)—may be a product of their marked success in competing for photosynthetic space with other early-evolving microbes. Unlike the oxygen-producing photosynthesis based on chlorophyll *a* in cyanobacteria, that in all other photoautotrophic prokaryotes is anoxygenic and bacteriochlorophyll based. Because biosynthesis of bacteriochlorophyll is inhibited by molecular oxygen (67), oxygen-producing cyanobacteria would have rapidly supplanted oxygen-sensitive anoxygenic photoautotrophs throughout much of the global photic zone. As a result of the ease of their global dispersal and their success in competing for photosynthetic space, cyanobacteria presumably expanded into a broad range of habitable niches during an early, evidently rapid phase of adaptive radiation (62), evolving to become exceptional ecologic generalists. Thus, the ecologic versatility of cyanobacteria appears to hark back to an early stage of planetary history when they established themselves as the dominant primary producers of the Precambrian ecosystem.

In view of their evolutionary history, it is perhaps not surprising that Simpson's rule of survival of the (ecologically) relatively unspecialized is applicable to cyanobacteria, numerous taxa of which qualify as so-called living fossils. According to Stanley, such extraordinarily long-lived organisms "are simply champions at warding off extinction" (ref. 70, p. 280). If so, as has been previously suggested (ref. 11, p. 598), the "grand champions," over all of geologic time, must be the hypobradyletic cyanobacteria!

#### A Bipartite View of the History of Life

In broadbrush outline, biotic history thus seems divisible into two separate phases (2, 3), each characterized by its own tempo and mode, each by its own set of evolutionary rules (Fig. 1).

During the shorter more recent Phanerozoic eon, the history of life was typified by the horotelic evolution of dominantly megascopic, sexual, aerobic, multicellular eukaryotes based on alternating life cycle phases specialized either for reproduction or for nutrient assimilation. Changes in the dominant (commonly diploid) phase resulted chiefly from structural modification of organ systems used to partition and exploit particular environments. In large part as a result of this ecologic specialization, the Phanerozoic was punctuated by recurrent episodes of extinction, each followed by the adaptive radiation of surviving lineages.

In contrast with Phanerozoic evolution, much of the earlier and decidedly longer Precambrian history of life was typified

by the hypobradyletic evolution of dominantly microscopic, asexual, metabolically diverse, and commonly ecologically versatile prokaryotes, especially cyanobacteria. Evolutionary innovations were biochemical and intracellular. Once established, lineages exhibited long-term stasis. Extinction occurred rarely among prokaryotic ecologic generalists, evidently becoming a significant evolutionary force only late in the Precambrian and primarily affecting ecologically relatively specialized, large-celled eukaryotic phytoplankters (71–74).

Although as yet incompletely documented, this bipartite interpretation of evolutionary history seems consistent with the fossil record as now known. It remains to be established whether it, like Simpson's *Tempo and Mode* (1), will stand the test of time.

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